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GROWTH AND DIFFERENTIATION IN APRICOT TREES

BY
H. S. REED

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I. INTRODUCTION

The 'habit of growth' of a species or variety is a character to which reference is often made in botanical discussions. The pattern of an organism is the result of a process of growth and differentiation which is largely an expression of factors inherent in that organism. Growth produces not only an increase in size; it is accompanied as well by a complex differentiation of the organism. Nothing could be more important than an investigation of these processes in order to discover the fundamental principles which govern them. Those who are interested in the broader problems of biology will be concerned with the laws of growth, while those who are interested in the art of horticulture may gather from such a study something that is fundamental in fruit production.

There are two well recognized methods of attacking the problem of growth: the experimental and the observational. So far as the dynamics of growth are concerned, the experimental method of study, dealing largely with factors which control processes, may be expected to yield useful information. But when dealing with growth in relation to differentiation, and with the problem of correlation of different members of an organism, the observational method is of great importance, and it is this method that was employed in the present investigation.

The writer has shown in earlier papers that the growth of an organism, or organ, proceeds in a definite, orderly fashion, and that it is possible to express the rate of growth by a mathematical equation. This contributes nothing, of course, to our knowledge of the causes of growth, but does emphasize the fact that the form and the function of organisms, though variable, nevertheless are not outside the realm of exact science. With respect to apricot branches, it is known that their growth in length conforms to an equation in which the size is shown to be a definite function of the time.

* Paper No. 112, University of California, Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, California.

In the present paper variability and differentiation in apricot branches will be discussed at length. In respect to length of main axis and percentage of buds which overcame dormancy in the first season, variability was not excessive. In respect to other characters, however, variability was very great. Amount of growth, for example, is apparently largely determined by fortuity of position, because of varying reaction to heat and light. Diverse types of development are manifested by orthotropic and plagiotropic branches. A large part of the material and energy at the disposal of the branch is devoted to forming structures which, though subsidiary, exceed in size the main axis of the branch. It will be important, therefore, to investigate the quantitative relationships between branches and their members.

The greatest growth of laterals is produced on the most vigorous branches. The unity of the organism is demonstrated by the close relationship between the vigor of the branch and the vigor of the laterals produced on it. Speaking in chemical terms, we might say that variations in the quantity of growth-promoting substances or of tissue-forming materials are uniformly distributed throughout a branch. Although the terminal portion of a branch exerts a dominant influence over the development of the subterminal portions, the factors which tend to promote growth in one region tend also to promote growth in another.

The most casual observer cannot help noticing, in figure 1, the three distinct groups of laterals on the branches. Between adjacent groups there are many buds whose dormancy was not broken during the first growing season. The quantitative characters of these groups have been of great interest in the study of the pattern of the apricot branches, because they indicate a certain definite distribution of mass along the axis of the branch.

A former study of growth in young pear trees⁹ showed that the size of a shoot is a function of its position on the mother shoot. The present study shows that the shape and size of these groups of laterals is a function of their position on the main axis; in other words, that their specific method of development is a quantitative character. This relationship seems to be highly important and to support the idea that the growth process (in its simplest form) brings about a definite distribution of matter in space which takes the form of a characteristic pattern. The position and size of the laterals on the branches must be regarded as the result of a process of differentiation which as yet has been but little studied with reference to its quantitative characters.

Herbert Spencer¹² has stated the problem succinctly.

The morphological differentiation which thus goes hand in hand with morphological integration is clearly what the perpetually-complicating conditions would lead us to anticipate. Every addition of a new unit to an aggregate of such units must affect the circumstances of the other units in all varieties of ways and degrees, according to their relative positions, must alter the distribution of mechanical strains throughout the mass, must modify the process of nutrition, must affect the relations of neighboring parts to surrounding diffused actions; that is, must initiate a changed incidence of forces tending ever to produce changed structural arrangements.

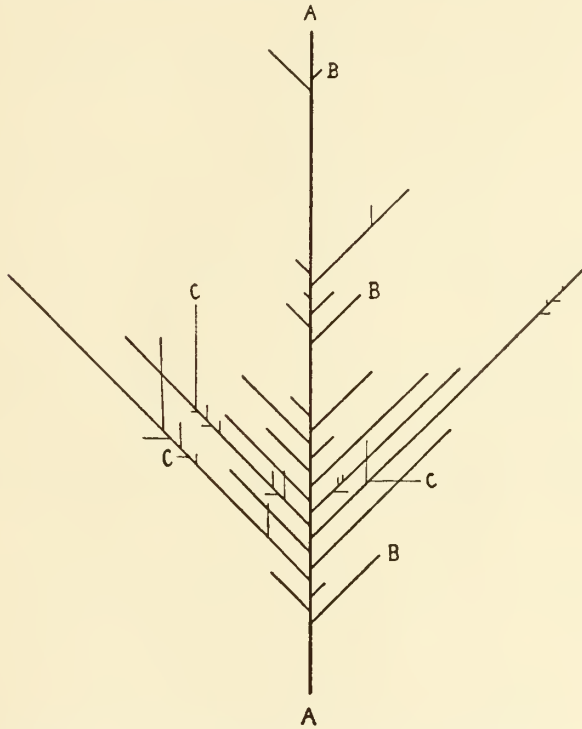


Fig. 1. Diagram of a young apricot branch showing the type of material used in the study. AA, branch axis; B, primary lateral; C, secondary lateral.

The data to be presented afford strong evidence that the number of laterals per branch is largely determined by factors which impose a condition of dormancy upon the buds of most of the nodes. The greater number of branches have relatively few laterals. This condition is of obvious interest to horticulturists, who find it necessary to employ various means of promoting the formation of laterals. So far as possible, the factors which influence the production of laterals have been studied, and the need for further investigation indicated.

The production of flower-buds on the branches is another question of biological interest. The number of blossoms on a branch is necessarily dependent upon the number of laterals it produces, but long laterals show no tendency to be more prolific in blossoms than their shorter neighbors. One important exception to this relation was found in the case of primary laterals, where there appeared to be a distinct group of relatively long laterals possessing from 50 to 110 nodes, in which the majority produced less than five blossoms each. This group might be regarded as being predominantly vegetative in activity, while the other laterals were both vegetative and reproductive in function. There is a notable difference in the number of blossoms per lateral of different groups, which is probably caused in large measure by differences in age of the several groups.

If we assume that there is some sort of an equilibrium in the tree between forces producing vegetative and reproductive growth, we may understand better the various correlations between blossoms and other characters which are to be studied in the following pages. Speaking broadly, we may say that each lateral appeared to produce about the same number of blossoms as its neighbors of approximately the same age, and that the number of blossoms on a lateral was more or less independent of the number of nodes which the lateral possessed. In other words, it may be a matter of indifference to the fruit grower whether the branches have long laterals or short laterals so far as the capacity of the trees to produce 'fruit buds' is concerned.

In the apricot trees studied the equilibrium between forces influencing vegetative and reproductive growth varied, apparently, only between limits. The variability in the number of blossoms per branch is large and may possibly indicate that the equilibrium between forces is relatively unstable. The average number of blossoms per branch was 360, but the actual numbers ranged from 50 to 1200. This wide variability may have resulted from the fact that we were dealing in this case solely with young branches produced in the preceding season. The data give some evidence on the opposition of growth processes to fruit-bud formation. It was found that, while the distal region of the branch was actively growing, the physiological functions of that region were opposed to the formation of energy centers which produce fruit-buds. In the proximal region, where vegetative growth had largely ceased before the end of the season, the formation of fruit buds was not opposed by other functions.

II. DESCRIPTION OF THE MATERIAL

The data for the present study were obtained from four-year-old apricot (*Prunus armeniaca*) trees of the horticultural variety known as Royal. The trees stand in an orchard at the Citrus Experiment Station, Riverside, California. Measurements were taken of 79 branches which had grown in the preceding year. The branches were selected from 36 different trees scattered over the orchard in such a way as to give a fairly random distribution. Figure 1 shows in a diagrammatic way the morphology of a typical branch selected from the population studied.

There are advantages and disadvantages in working with material from a clonal variety which, for many years, has been propagated by budding. A budded tree has something of the nature of a dual organism, since it is growing upon the root of a seedling tree. The clonal quantitative characteristics may be somewhat modified by the vigor of the stock upon which the variety is propagated, though it is doubtful whether a group of trees like these would have as great variability as a similar number of unbudded seedling trees. The Royal apricot probably originated in France. "This valuable sort was raised in the Royal garden of the Luxembourg, whence a plant was sent to the [Royal Horticultural] society [of London] by M. Hervy, the Director. It fruited in the Garden in 1828 and was then figured in the Pomological magazine."¹⁴

In the discussion, the following terms will be used: 'branches' are the 79 shoots which make up the population under study; 'mother shoots' are the year-old limbs on which the population grew; 'primary laterals' are the shoots which grew from certain nodes of the branches; 'secondary laterals' are shoots which grew on the primary laterals.

The mother shoots were pruned by the amputation of about three-fourths of their length in the early spring of 1920. The 79 branches upon which this study is based grew during the following season from buds situated a short distance back of the points at which the mother shoots had been amputated. The favorable position of the branches, as well as the severe pruning of the mother shoots, unquestionably had much to do with this vigorous growth.

The primary and secondary laterals were developed as the branch grew and reached a total length which averaged 7 to 8 times the length of the main axis on which they were borne (fig. 1).

During the growing season measurements were made each week to determine the length of the branches. The length of the primary and secondary laterals was not determined during the growing season. At the end of the growing season an extensive series of measurements was made covering the length and circumference of the branches, number of laterals, number of dormant buds, and number of blossoms. These measurements of the shoot systems with their adherent laterals serve as a basis for the present study.

The vegetative shoots of the apricot tree constitute very favorable material for the study of growth relationships. Previous papers from this laboratory^{6, 7, 8} have presented some of the salient features in the growth of shoots like those here studied. Except for the vigor and rapidity of their growth these shoots differed in no essential from those of other fruit trees which have been under observation.

In the early part of the growing season the apricot shoots grow very rapidly, making about half their season's growth in the first seven to nine weeks. The rate of growth usually attained its first maximum in the fifth or sixth week of the season, then gradually declined with more or less irregularity to about the fourteenth week; it reached a second maximum about the seventeenth week and fell to its final minimum from the twenty-fifth to the twenty-eighth week. This tendency to cyclic growth is characteristic of many trees and is well illustrated by the growth of the apricot shoots.

The growing season for apricot shoots in the locality mentioned usually begins in March and extends to some time late in autumn. It is therefore necessary to make measurements of the elongation over a total period of eight or nine months.

Results of an earlier investigation⁶ showed that there were three cycles in the seasonal growth of a sample of vegetative shoots and that the growth in each cycle could be quantitatively expressed by the equation

$$\log \frac{x}{a-x} = K(t-t_1).$$

In this case x is the length of the shoots at time t ; a is their final length; t_1 is the time at which the shoots have been made one-half of their final length a ; and K is a constant. This equation has been found to express the growth of both plants and animals, and is useful in analyzing the growth process. The rate of growth of apricot shoots is definitely related to the final length a , with distinct quantitative differences between shoots of various length through the entire season.⁷

Pruning the trees severely in the dormant period had a marked influence upon the sap concentration and the rate of growth of vegetative shoots in the following season. Sap concentration on rapidly growing shoots was usually much less than on slowly growing shoots, and showed a descending gradient from the apex toward the base of the shoots.⁸

The final measurements of the branches and their parts were taken with the assistance of Mr. F. F. Halma and Dr. A. R. C. Haas in the spring of 1921 just before the beginning of growth. Not only length and number of buds were recorded for each branch and lateral, but the position of each lateral on the shoot which bore it was recorded. Table 1 presents the data in a condensed form.*

* The writer realizes the advisability of publishing the original data, but, for reasons of economy, is unable to do so. The original figures have been preserved and may be consulted by anyone who wishes to use them.

TABLE 1
SUMMARY OF DATA ON APRICOT BRANCHES

Branch No.	Angle from perpendicular (dgrs.)	Location	Length (cm.)	Total no. of nodes	No. dormant nodes	No. primary laterals	No. secondary laterals	Length of all primary laterals (cm.)	Length of all secondary laterals (cm.)	No. of blossoms
1	30	NE	246	148	116	32	21	1029	198	320
2	50	S	257	130	101	29	59	1473	1128	1066
3	50	SE	241	145	116	29	13	1133	111	495
4	90	SE	235	138	103	35	20	1057	269	383
5	45	N	237	126	82	44	62	2021	1124	714
6	80	SE	263	153	120	33	79	2016	1304	347
7	50	W	195	114	86	28	41	1164	686	238
8	30	NW	230	121	57	64	136	3078	1852	503
9	90	SE	224	128	110	18	19	475	177	249
10	90	S	233	125	84	41	71	2011	1307	534
11	60	NE	267	136	97	39	77	2765	1509	437
12	75	SW	220	126	93	33	51	1626	715	235
13	90	NW	227	137	103	34	12	1095	108	192
14	90	S	263	134	99	35	109	2635	1795	307
15	75	N	251	145	110	35	49	1505	964	231
16	45	NE	267	149	92	57	133	2816	1903	753
17	45	SE	289	164	100	64	127	2765	2848	293
18	90	E	270	154	126	28	60	1659	775	527
19	30	W	280	178	126	52	103	2804	1755	391
20	45	S	305	148	92	56	117	3169	2157	612
21	80	SW	231	127	96	31	30	1677	333	374
22	60	E	260	137	98	39	39	1739	462	302
23	90	SE	223	144	120	24	19	1005	389	166
24	75	N	152	77	39	38	13	866	93	134
25	50	SW	223	134	91	43	24	1248	227	358
26	0	SE	218	138	78	60	69	1672	846	547
27	90	E	221	113	88	25	4	703	36	115
28	45	SW	227	124	98	26	18	1013	173	514
29	85	SW	260	129	95	34	10	955	173	450
30	85	S	260	134	100	34	25	860	424	530
31	30	N	283	151	105	46	41	1608	536	645
32	90	S	137	82	64	18	8	338	57	298
33	85	NW	211	110	78	32	49	1510	683	523
34	70	S	238	129	98	31	22	1199	206	468
35	80	W	202	111	76	35	19	1077	163	491
36	90	SE	180	75	48	27	0	760	0	162
37	50	SE	191	112	96	16	1	371	14	185
38	90	SW	216	109	78	31	2	716	42	259
39	90	W	229	138	112	26	2	583	13	27
40	45	SE	253	144	101	43	22	2004	288	104

TABLE 1—(Continued)

Branch No.	Angle from perpendicular (dgrs.)	Location	Length (cm.)	Total no. of nodes	No. dormant nodes	No. primary laterals	No. secondary laterals	Length of all primary laterals (cm.)	Length of all secondary laterals (cm.)	No. of blossoms
41	80	SE	235	141	108	33	13	1031	144	90
42	50	S	211	115	74	41	5	888	78	146
43	90	E	211	87	67	20	4	377	19	151
44	80	S	256	144	110	34	12	1584	222	230
45	40	SE	312	157	103	54	100	2643	1576	639
46	90	SW	218	117	104	13	0	262	0	159
47	80	E	225	122	95	27	0	578	0	285
48	70	E	258	135	98	37	31	1059	484	283
49	70	S	216	130	108	22	11	509	235	108
50	75	W	253	154	123	31	11	846	170	190
51	45	E	255	121	86	35	31	1207	582	451
52	85	SE	263	133	104	29	15	1098	194	270
53	90	W	230	136	120	16	2	381	21	216
54	45	NE	265	130	82	48	46	2148	778	899
55	90	SE	249	124	104	20	4	583	66	240
56	90	SE	226	124	102	22	1	510	5	198
57	90	S	212	131	107	24	4	670	29	376
58	90	E	200	107	88	19	0	348	0	139
59	30	W	252	117	84	33	21	1279	231	258
60	45	NE	252	131	69	62	72	2449	1081	1197
61	50	S	226	128	82	46	93	2418	1069	574
62	30	S	209	117	71	46	37	1354	217	383
63	45	E	191	86	59	27	0	706	0	129
64	80	E	225	115	68	47	16	1555	256	472
65	45	NE	256	124	76	48	30	1296	304	523
66	50	E	253	129	103	26	8	762	75	190
67	80	E	252	126	86	40	27	1319	331	342
68	90	SW	217	109	84	25	7	606	88	252
69	45	SE	253	143	103	40	34	1369	378	207
70	45	SE	274	150	95	55	63	2323	944	599
71	45	S	277	136	94	42	41	1778	534	422
72	80	N	213	119	82	37	20	913	319	360
73	20	E	250	133	88	45	50	2239	492	346
74	15	N	260	144	98	46	78	2452	1000	615
75	50	SE	261	134	103	31	18	909	264	86
76	90	S	211	126	108	18	5	454	35	44
77	90	SE	143	61	27	34	16	1304	185	135
78	50	NE	229	102	71	31	0	433	0	56
79	30	E	271	128	77	51	14	1531	134	255

III. RATE OF GROWTH OF THE BRANCHES

The mean length of the shoots for each week is a convenient and reliable index of their rate of growth. Measurements of the length of these 79 branches were made at seven-day intervals throughout the growing season. Their rate of growth is of interest in the present discussion chiefly because it shows the existence of two distinct cycles

TABLE 2

THE GROWTH OF THE MAIN AXIS OF THE BRANCHES. COMPARISON OF OBSERVED MEAN LENGTH AND CALCULATED VALUES. VALUES FOR THE FIRST CYCLE

COMPUTED FROM $\text{LOG} \frac{x}{190-x} = .147 (t-6)$; FOR SECOND CYCLE

$\text{LOG} \frac{x-170}{240-x} = .201 (t-17.3)$

First Cycle				Second Cycle			
<i>t</i>	<i>x</i> (obs.)	<i>x</i> (calc.)	θ	<i>t</i>	(<i>x</i> -170) obs.	(<i>x</i> -170) calc.	
(wks.)	(cm.)	(cm.)	(cm.)	(wks.)	(cm.)	(cm.)	(cm.)
0	22.0	13	2.0	8.4	6.4
1	17.5	29.5	12.0	15	17.3	17.9	0.6
2	32.8	39.0	6.2	17	31.3	32.6	1.3
3	45.6	50.5	4.9	19	47.7	48.1	0.4
4	61.7	64.0	2.3	21	58.8	59.3	0.5
5	81.6	79.0	-2.6	25	67.3	68.0	0.7
6	94.9	95.0	0.1	38	68.6	69.8	1.2
7	108.2	108.1	-0.1	Root-mean-square deviation			2.55
8	121.5	126.0	4.5				
9	135.9	139.5	3.6				
10	147.1	151.1	4.0				
11				
12	166.1	168.0	1.9				
13	172.0	173.7	1.7				

Root-mean-square deviation 4.78

of growth, the first covering the period of 13 weeks in which the most rapid elongation occurred, the second covering the remainder of the growing season. Table 2 shows the observed mean length of the branches at weekly or bi-weekly intervals for 38 weeks and also the length computed from the equation¹³

$$\log \frac{x}{a-x} = K (t-t_1).$$

The actual equation for the first cycle was

$$\log \frac{x}{190-x} = .147 (t-6).$$

The equation for the second cycle assumes that the ordinate and the abscissa have been removed to a new point of origin. The new values of x were obtained by subtracting 170 from each of the observed values of x . The actual equation was

$$\log \frac{x-170}{240-x} = .201 (t-17.3).$$

The graph (fig. 2) shows that the agreement between the computed and observed values of the mean length is satisfactory.

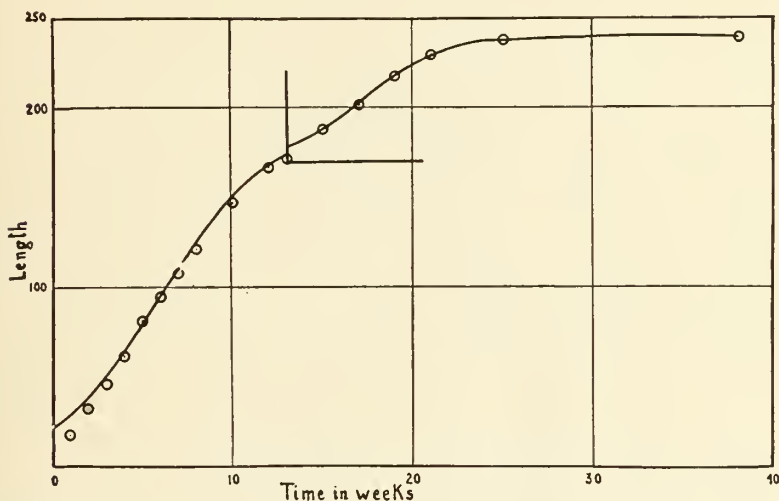


Fig. 2. Growth curve of the population of branches. The small circles represent observed mean length of branches, the curves were calculated from the equations: first cycle, $\log \frac{x}{190-x} = .147 (t-6)$; second cycle, $\log \frac{x-170}{240-x} = .201 (t-17.3)$

It may be of interest to note that the appearance of primary laterals was not coincident with the termination of the first growth cycle. The time at which these laterals first appeared ranged from the third to the seventh week, the mean time being 4.31 weeks from the beginning of the growing season. The relations appear to be different from those described for the growth of roots by Priestley and Pearsall,⁵ who reported that the appearance of secondary or of tertiary roots is concomitant with a lag in the growth curve.

The validity of the foregoing equation may be tested further by comparing the observed and computed increments in length during the growing season. The foregoing equation, when differentiated, becomes

$$\frac{dx}{dt} = kx(a - x)$$

where $k = \frac{K}{a}$ and the other letters have their former significance.

The computed values $\frac{dx}{dt}$ and the observed values of S are given in table 3. The latter were smoothed by the method commonly used for such cases according to the equation

$$S = \frac{1}{2} (x_{t-1} + x_{t+1})$$

TABLE 3
GROWTH RATE OF APRICOT BRANCHES AS SHOWN BY THEIR WEEKLY
INCREMENT IN LENGTH

First Cycle				Second Cycle			
t	$\frac{dx}{dt}$	S	θ	t	$\frac{dx}{dt}$	S	θ
(wks.)	(cm.)	(cm.)	(cm.)	(wks.)	(cm.)	(cm.)	(cm.)
0	6.8	0	6.8	13	3.4	7.7	-4.3
1	8.7	8.8	-1	15	6.2	7.5	-1.3
2	10.9	10.8	1	17	8.1	7.9	.2
3	13.0	10.7	2.3	19	7.0	6.3	.7
4	14.7	16.4	-1.7	21	4.2	5.4	-1.2
5	15.8	14.7	1.1	25	.9	2.1	-1.2
6	15.9	16.6	.7	38	1	1	0
7	15.0	13.3	1.7	Root-mean-square deviation 1.84			
8	13.4	13.8	-.4				
9	11.3	12.3	1.0				
10	9.1	11.9	-2.8				
11	7.1	10.4	-3.3				
12	5.4	7.7	-2.3				
13	4.0	7.7	-3.7				
14	2.9	6.8	-3.9				
15	2.1	7.5	-5.4				
17	1.1	7.9	-6.8				
19	.6	6.3	-5.7				
21	.3	5.4	-5.1				

Root-mean-square deviation 3.61

The agreement of the actual and computed values is shown in figure 3. The curves for the two cycles overlap, indicating that the two phases of growth in these branches are not sharply separated from each other. Consequently we must add together the computed values where the curves overlap to approximate the summation of the two cycles. The course of these summations is shown by the dotted line, and the observed values agree well with them.

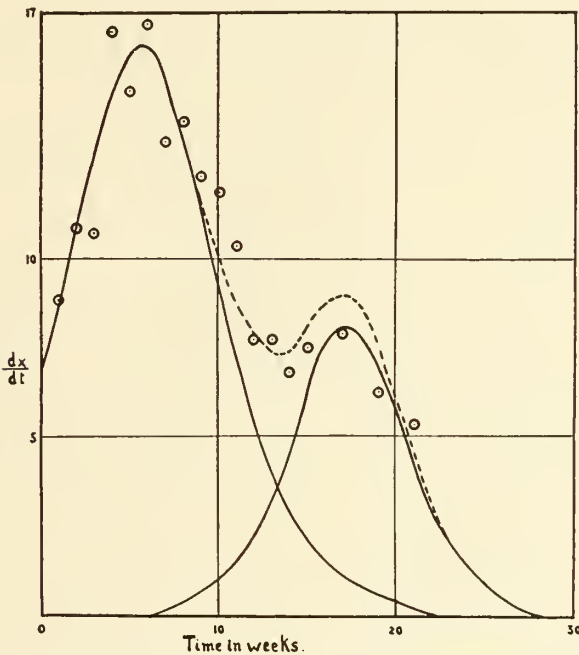


Fig. 3. Growth rate of apricot branches, showing the two overlapping cycles. The curves were calculated from the equations: first cycle,

$$\frac{dx}{dt} = .00077x(190 - x), \text{ second cycle, } \frac{dx}{dt} = .00084(x - 170)(240 - x).$$

The dotted line is the sum of the overlapping portions of the curves. Small circles represent mean weekly increments in length.

These considerations show that the main axis of the apricot branches grew during the entire season in two cycles at perfectly definite rates each of which resembles the rate of an autocatalytic reaction. They show furthermore that the equations may be profitably used to analyze the season's growth.

IV. MORPHOLOGY OF THE BRANCHES

The branches under discussion (fig. 1 gives an idea of the shape they assumed) were selected in early spring at a time when they were only a few centimeters long. They developed from buds near the distal ends of the mother shoots and stood in positions where they had prospects of unhampered development. We may regard this population as representative of shoots which make rapid growth during the first season. Statistics for the salient characters of these branches are given in table 4.

The length of the branches ranged from 137 to 312 cm. and had a mean of 235.95 ± 2.47 cm. The coefficient of variability is not greater than that commonly encountered in the measurement of biological material.

These branches were less variable with respect to their length than to any other character measured. The frequency distribution of the branches with respect to length is shown in figure 4. The frequency polygon is fairly symmetrical with respect to its mean and does not depart widely from the type of polygon which represents a random distribution of characters in biological material. In certain respects the variability in elongation is like that previously described⁹ for the shoots of young pear trees.

The total number of nodes on a branch shows a mean of 127.69 with a coefficient of variability of 15.65. The number of nodes on a branch is closely related to its length, consequently the coefficients of variability of length and bud number are not widely different.

The apricot branches have a phyllotaxis of two-fifths. Each node produces from one to three buds only one of which gives rise to a vegetative shoot. The central bud of the group usually develops, the others remain dormant, at least during the first year.

The production of primary and secondary laterals is one of the important activities of the apricot branch. The number of primary laterals ranged from 13 to 64 with a mean of 37.00 ± 1.19 . The distribution of the primary laterals is rather asymmetrical and shows a tendency to skewness toward the higher class values (fig. 5). This distribution is also reflected in the large coefficient of variability (table 4).

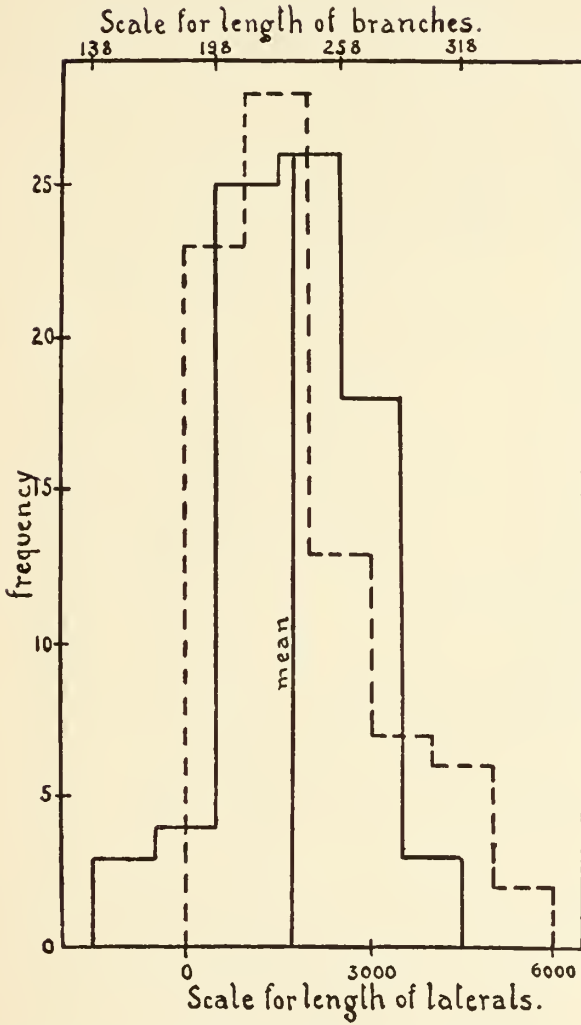


Fig. 4. Frequency distributions for length of branches and combined length of laterals for each branch. The means of the two histograms are superposed. Length of branch, —; combined length of laterals, - - -.

TABLE 4
DEVELOPMENT OF BRANCHES AND OF THEIR PARTS

	Mean	Standard deviation	Coefficient of variability
Length of branches.....	235.95 ± 2.47 cm.	32.49 ± 1.75 cm.	13.77 ± .76
Circumference at base.....	8.90 ± .17 cm.	2.16 ± .12 cm.	24.27 ± 1.39
Number of nodes per branch.....	127.69 ± 1.52	19.95 ± 1.08	15.65 ± .87
Number of dormant nodes per branch.....	92.44 ± 1.44	18.89 ± 1.02	20.43 ± 1.15
Number of primary laterals per branch.....	37.00 ± 1.19	15.69 ± .85	42.41 ± 2.67
Percentage of nodes which developed primary laterals.....	27.51 ± .70	9.18 ± .50	35.71 ± 2.16
Number of secondary laterals per branch.....	35.00 ± 2.57	33.78 ± 1.82	96.51 ± 8.86
Total length of all laterals per branch.....	1844.94 ± 76.69 cm.	1010.57 ± 54.57 cm.	54.78 ± 3.70
Ratio of total length of all laterals to length of branches which bore them.....	7.63 ± .36	4.72 ± .25	61.87 ± 4.42
Number of blossoms per branch.....	360.26 ± 16.62	217.55 ± 11.67	60.39 ± 4.28
Length of primary laterals.....	51.17 ± 1.11 cm.	51.40 ± .79 cm.	100.45 ± 2.66
Length of secondary laterals.....	15.74 ± .35 cm.	18.98 ± .24 cm.	120.58 ± 3.06

The number of secondary laterals produced on the primary laterals ranged from 0 to 136 with a mean of 35.00 ± 2.57 per branch. The close agreement between the mean number of primary and of secondary laterals may or may not have a significance. Further investigation is necessary before any definite statement can be made. The distribution of the number of secondary laterals is more asymmetric than that of the primary laterals. Figure 5 shows that the greatest frequency occurs in the class having the lowest value. From this class the frequencies are successively less in the direction of the higher class values. The one-sided distribution is also reflected in the very large coefficient of variability.

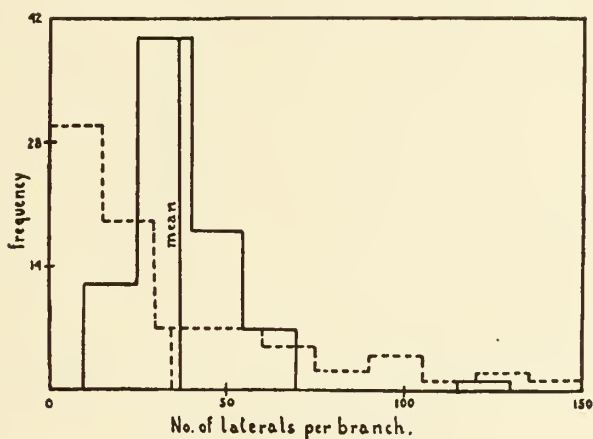


Fig. 5. Frequency distribution for primary and secondary laterals. Primary laterals, —; secondary laterals, - - -.

The nature of the variability in the number of laterals directs attention to the nature of the factors which determine their production. An apricot shoot does not arise from a lateral bud except where the conditions which impose dormancy are overcome, hence the number of laterals may be an index of the factors which overcome dormancy. The variability in the production of laterals indicates that the forces which overcome dormancy in the buds are conditioned, not upon factors of environment, but upon factors inherent in the tree. If factors of environment determined the release from dormancy, we should expect to find a more nearly normal type of distribution.

It is interesting to note that there is not a high degree of association between the length of branch and the total number of laterals which it bore. We may designate number of laterals as a , total length

of laterals as b , and length of branch on which they were borne as c . The coefficient of gross correlation is

$$r_{ac} = .337 \pm .067$$

The coefficient of partial correlation taking into consideration the length of the laterals is

$${}_{ac}r_b = -.313 \pm .013$$

which means that, if all laterals were the same length, there would be a negative association between length of branch and number of laterals produced.

A comparison of figures 4 and 5 shows that the frequency distribution of total length of all laterals per branch is somewhat different from that representing the numbers produced. The ratios of the first to the second character have a mean of $7.63 \pm .36$ (table 4). The distribution of total length is not strictly symmetrical, as shown by the graph in figure 4, there being a distinct tendency for the polygon to skew toward the higher class values. In figure 4 the polygon representing distribution of total length of laterals per branch is located in such a position that its mean is superposed on that of the length of branches. The two polygons show a fair degree of correspondence.

The correspondence between the two characters may better be determined by their coefficient of correlation. We may designate number of laterals per branch as a , length of branch on which they were borne as c , and total length of laterals as d .

$$r_{cd} = .700 \pm .040$$

This indicates a high degree of positive relationship between length of branch and length of laterals produced upon it. Since the number of laterals on branches was itself a variable, we may determine the coefficient of partial correlation, which expresses the correlation in case each branch had the same number of laterals. This is

$${}_{cd}r_a = .665 \pm .042.$$

The value of this coefficient indicates a very strong relationship between the growth capacity of a branch and that of its laterals.

The foregoing discussion may be summarized in the following four paragraphs:

1. The correlations indicate that the longer branches tended to have more laterals and longer laterals, hence it is likely that the position of these shoots on the tree markedly affected the growth capacity of the branches as wholes.

2. The marked difference between the frequency distribution of branches for primary laterals and that for secondary laterals doubtless depends largely on the age factor resulting from the position of the latter on primary laterals; this factor crowded a great part of the latter distribution into the zero class.

3. More generally, the skewness of several distributions suggests a large effect on these characters of a small and unbalanced group of factors conditioning growth.

4. Length of branch seems to have been relatively free from the influence of highly potent factors of asymmetrical effect, but this fact is probably the result in part of the original selection of branches for uniformity of positional growth factors. The farther the members produced get away from the initial leveling effect of that selection, the farther they lapse back into a condition of asymmetric distribution which, as we shall see later, seems to be a general characteristic of the differentiation of the tree.

The graphs together with the illustration (fig. 1) will help to give an idea of the sort of growth that characterizes these apricot branches. The discussion which follows will attempt to discover their quantitative relationships and to analyze growth in the light of these relationships. The work will proceed on the assumption that the size and development of the branches is the result of some dynamic agent acting upon certain raw materials which the tree acquired from its environment. Broadly stated, the problem is to discover something about the process by which the tree forms its diverse parts out of unorganized material.

Data on the influence of location and of direction of growth upon the growth and differentiation of the branches are given in table 5. The branches are classified with respect to the points of the compass. The 'north' class comprises branches which were located on the northwest, north, and northeast sides of the trees, and so for other locations. This broad classification necessarily involves some duplication, because, for example, shoots which were recorded as northeast were included both in the north and in the east classes. This duplication undoubtedly operates to minimize differences between the adjoining classes, yet it cannot vitiate comparisons between opposite sides of the trees.

TABLE 5
INFLUENCE OF LOCATION AND POSITION ON DEVELOPMENT OF BRANCH

Influence of location	No. of branches in each class	Length (cm.)	No. of primary laterals	Ratio of primary laterals to total no. of nodes (per cent)	No. of blossoms per branch	Mean ratio of all laterals to branches (length)
NW-N-NE.....	15	240.00 \pm 3.55	42.67 \pm 1.79	34.33 \pm 1.52	502.83 \pm 50.38	10.23 \pm .89
NE-E-SE.....	40	241.50 \pm 3.31	36.25 \pm 1.38	28.37 \pm 1.12	347.0 \pm 24.92	7.33 \pm .49
SE-S-SW.....	41	236.10 \pm 3.71	34.22 \pm 1.27	25.90 \pm .95	329.99 \pm 20.77	7.24 \pm .48
SW-W-NW.....	18	231.67 \pm 3.52	33.89 \pm 1.90	25.61 \pm 1.35	316.17 \pm 22.68	7.06 \pm .80
Influence of position of branches						
0°-30° from perpendicular.....	9	251.67 \pm 6.19	48.11 \pm 2.30	33.11 \pm 1.97	435.61 \pm 29.90	10.33 \pm 1.18
30°-60° from perpendicular.....	27	249.81 \pm 3.86	30.52 \pm 1.55	30.52 \pm .68	453.20 \pm 37.02	9.24 \pm .64
60°-90° from perpendicular.....	42	226.67 \pm 3.15	29.14 \pm .81	24.38 \pm .94	276.88 \pm 14.22	5.76 \pm .37

The four classes of branches show no striking differences in mean length attributable to location. The mean number of primary laterals per branch ranged from 33.89 ± 1.90 in the west class to 42.67 ± 1.79 in the north class. Their difference is 8.78 ± 2.62 and may be regarded as significant since $\frac{D}{E_d} = 3.35$. The means of the other classes are not significantly different.

The mean ratio of primary laterals to total number of buds (index of lateral production) in the case of the north class indicates a significant difference from those on the other sides of the tree. This difference might have been predicted inasmuch as we have noted that the mean number of primary laterals on branches on the north side of the trees was a maximum while the mean length of the branches on which they grew was approximately the same as those in other classes.

The mean number of blossoms per branch shows no significant difference between different classes except in the case of the north class. The mean for this class is so much greater than the others that we must recognize a real difference in spite of the large probable error attached thereto: the branches in the north class appear to differ from those in the other classes in the possession of more primary laterals (both relatively and absolutely) and in the production of more blossoms. In other words, the process of differentiation seems to have gone farther in these branches. We must not, however, lose sight of the fact that the north class contains only 15 variants and that the reliability of the mean is correspondingly less.

The direction which the main axis of the branch maintains with respect to the perpendicular is known to exert a marked influence upon its form and function. The second part of table 5 presents some determinations made upon branches classified according to their position at the end of the growing season. I realize that the classification is not strictly accurate, because many branches which were vertical during the first part of the growing season changed their direction as time went on. Weight of the branch and competition for light are among the causes of change of direction. Indeed the greater number of variants in the most nearly horizontal class suggests that the population of this class increased at the expense of the more nearly vertical classes.

No definite statements can be made with respect to the mean length of the three classes of branches although one is inclined to believe that it is actually shorter in the 60° – 90° class than in the others. Those

familiar with the training of fruit trees know that horizontally placed shoots do not attain so great a length, in the same time, as do upright shoots.

The number of primary laterals was considerably greater on the upright branches than upon those of the other two classes, and least upon those in the 60° – 90° class. I think it only logical to assume that these differences reflect in large measure the effects of some growth-inhibiting agency whose action on horizontal shoots and cuttings has been previously described.^{10, 11} The development of laterals on these branches would also be influenced by the degree of success attained by the branch in its competition for light and by other growth promoting agencies.

The ratio of primary laterals to the total number of nodes on the branches is considerably smaller in the 60° – 90° class, indicating that the development of lateral buds is in some way retarded on these branches.

Another relationship which shows the effect of the direction of growth is that which exists between the length of the branch and the total length of all laterals. The ratio between these quantities ought to indicate the relative differentiation which a branch has undergone. These figures show that the most nearly upright branches had the highest ratio. Those which stood in the intermediate position, 30° – 60° , had a somewhat smaller ratio, but those most nearly horizontal had the smallest ratio. This condition calls attention to the usual differences in development between orthotropic and plagiotropic branches. The differences have been frequently mentioned in the literature and have been ascribed¹¹ to the action of a growth-inhibiting substance in the branch. Plagiotropic shoots are typically dorsiventral while orthotropic shoots are radial. This means that the buds on one side of the plagiotropic shoot are the only ones which reach any extensive development. As a result, the ratio of primary laterals to branch is smaller than in the case of upright shoots. The reasons for the smaller ratio may be two: first, the actual number of laterals is less; second, the laterals which develop are shorter. From an inspection of the figures in table 5 it seems that the first mentioned condition is principally responsible for the smaller ratio. It appears from data given in table 6 that the branches on the north side of the tree were somewhat less variable in the ratio of active to dormant nodes, and that the plagiotropic branches were more variable in this character than the orthotropic branches.

TABLE 6
EFFECTS OF LOCATION AND POSITION UPON THE PERCENTAGE OF NODES WHICH
PRODUCED PRIMARY LATERALS

INFLUENCE OF LOCATION	Mean	Standard deviation	Coefficient of variability
NW-N-NE.....	34.33 \pm 1.52	8.73 \pm 1.07	25.44 \pm 3.33
NE-E-SE.....	28.37 \pm 1.12	10.46 \pm .78	36.87 \pm 3.14
SE-S-SW.....	25.90 \pm .95	9.07 \pm .67	35.02 \pm 2.91
SW-W-NW.....	25.61 \pm 1.35	8.47 \pm .95	33.07 \pm 4.09
INFLUENCE OF POSITION OF BRANCHES			
0°-30° from perpendicular..	33.11 \pm 1.97	8.75 \pm 1.39	26.43 \pm 4.49
30°-60° from perpendicular..	30.52 \pm .97	7.44 \pm .68	24.38 \pm 2.37
60°-90° from perpendicular..	24.38 \pm .94	9.08 \pm .67	37.24 \pm 3.10

The number of blossoms which each class of branches produced in the following spring shows considerable variation (table 5). Here the difference between the 60°-90° branches and the others is of a magnitude that seems to be significant. Clearly, we cannot explain the difference by the fact that these branches were somewhat shorter than those of the other classes. Moreover, the difference in the number of blossoms should not be referred to the length of the branch, but to the total length of laterals on the branches of the three classes. J. P. Bennett has suggested that the ratio of blossoms to unit of lateral is greater in the 60°-90° class than in the others. The data given in table 7 show this to be true. The 0°-30° class of branches produced a combined

TABLE 7
RELATION OF THE DIRECTION OF GROWTH OF BRANCHES ON THE RATIO OF
SHOOTS TO BLOSSOMS

	Mean length of all laterals on the branch cm.	No. of blossoms per 100 cm. of laterals
Branches 0°-30° from perpendicular.....	2619	15.4
Branches 30°-60° from perpendicular.....	2455	18.2
Branches 60°-90° from perpendicular.....	1313	20.9

length of laterals which was about twice that of branches in the 60°-90° class. The number of blossoms per 100 cm. of laterals was greater, however, in the 60°-90° class. This suggests that conditions

in the 60°–90° class were more favorable for fruit-bud formation and decidedly less favorable for vegetative growth. The opposition between the vegetative and the reproductive activities of plants is so well known that extended comment is not necessary. The data here presented give a quantitative expression of the relationship for the apricot branches.

V. DORMANCY AND GROWTH OF BUDS ON THE BRANCHES

The average number of nodes on the branches measured was 127.69 ± 1.52 and the standard deviation was 19.95 ± 1.08 (table 4). The type of the distribution of nodes (fig. 6) and that of branch length are necessarily more or less similar, and both are skewed toward the lower class ranges.

The mean distance between nodes was approximately 1.85 cm., but in certain regions, especially near the proximal end, they were more closely grouped than in others. There is no doubt that the rate of growth of the main branch has an effect in spacing the nodes on its axis. The differences in spacing have not been measured for the present study.

Approximately 30 per cent of the nodes on the branch produced lateral shoots during the period when the branch was still making its first season's growth, while the rest remained dormant. The stoichiometry of the branch depends to a large extent upon the way in which the buds react, i.e., whether they remain dormant or grow. It is therefore important to investigate the question of growth and dormancy in these buds.

Each bud may be regarded as a center of potential energy in which there is located a quantity of labile compounds of carbon and nitrogen. Under certain conditions, processes of growth are initiated in the course of which these energy centers produce new structures. The amount of material synthesized at each energy center and its relation to the rest of the system may, to some extent, serve as an index of those dynamic factors with which we have to deal.

The ratio of primary laterals to all nodes expressed as a percentage gives the most obvious expression of lateral production. This ratio has been determined for each branch (table 4). The mean of all ratios is $27.51 \pm .70$. The frequency distribution of these ratios is shown in figure 7.

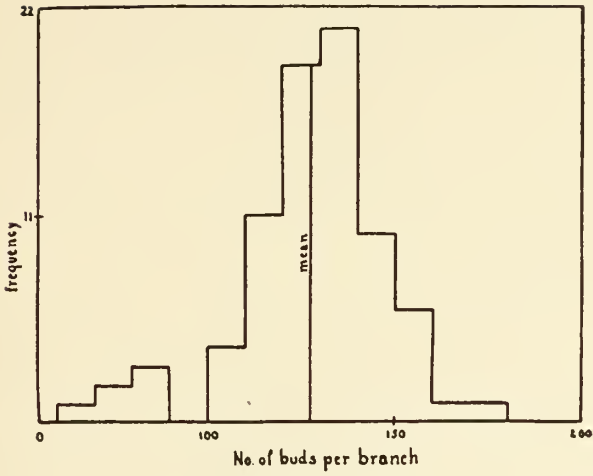


Fig. 6. Frequency distribution for number of nodes.

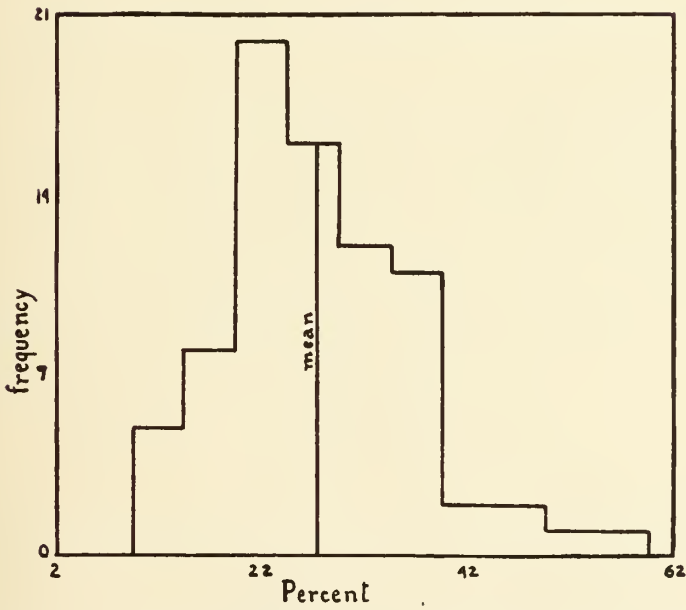


Fig. 7. Frequency distribution showing per cent of nodes from which primary laterals were produced.

This histogram shows some very important things about the variability in the percentage of nodes which produce primary laterals. In the first place, the skewness of the figure is pretty good evidence that the percentage of buds which developed was not entirely due to purely chance factors. Had that been the case the figure more nearly would resemble the normal curve of errors. In the second place, we find upon referring to table 4 that the coefficient of variability for the percentage of nodes which produced primary laterals is more than twice as large as the same constant of variability for the total number of buds.

These relationships seem to indicate that this problem of differentiation is not entirely simple; that no one factor determines whether a bud shall grow or remain dormant; but rather that the factors which overcome dormancy are much more variable in their effects than those which determine the formation of nodes upon the branch. It was seldom that more than 50 per cent of the nodes on a branch produced laterals and the modal value was only 24.29 per cent. Some of the conditions which operated to cause this variability in overcoming dormancy of the buds will be pointed out later.

In an earlier paragraph attention was called to the effect which location and position of the branch have on various phases of development. Table 6 also shows the effect of these factors upon the percentage of nodes which produced primary laterals. It will be seen that the branches on the north side of the trees produced a greater percentage of laterals than those on the other sides of the trees. The mean is appreciably larger than the means of other groups and the coefficient of variability is considerably smaller. The mean percentages of the other three groups show no significant differences.

When the branches are classified according to their declination from a perpendicular line we find differences in the percentages of buds which developed. The percentages in the classes 0° – 30° and 30° – 60° are not significantly different either in magnitude or variability, but the 60° – 90° class was significantly lower as to its mean and also more variable.

The percentage of dormancy in different regions on the branches is another measure of the distribution of growth stimuli. The nodes on the branches were tabulated in groups of 20 each and the percentage of dormancy determined for each group. Group 1–20 is the proximal group and group 161–180 is the distal group. The figures as given in table 8 show that great differences in the percentage of

dormancy existed in different regions. The lowest percentage of dormancy existed in group 21-40, in which only 19.05 per cent of the buds failed to develop. From this region the percentage of dormancy increased to 94.59 in group 81-100, dropped slightly in the next group, and rose gradually in succeeding groups to complete dormancy in the last group.

TABLE 8

PERCENTAGE OF DORMANCY IN NODES ON DIFFERENT REGIONS OF THE BRANCHES

	Groups								
	1-20	21-40	41-60	61-80	81-100	101-120	121-140	141-160	161-180
Percentage of dormancy.....	79.68	19.05	61.96	76.86	94.59	89.49	96.62	96.43	100.0

It is evident that the forces which broke the dormancy of the buds on these apricot shoots were not distributed in a regular gradient. The lowest group had a high percentage of dormancy, while the next group had the lowest percentage. Clearly we cannot refer the cause of such a distribution either to a simple axial gradient or to an age factor, except in the distal part of the branches. The data under discussion lead directly to the next point, viz., the number and position of primary laterals.

The relationship between the length of the branch and the number of nodes from which primary laterals were produced is a problem of some biological importance. The best method of expressing these relationships is by a series of correlations. The correlation coefficients ought to show whether a long or a short branch tends to produce more primary laterals. If we let l = the length of a branch; n = the number of nodes on a branch; and d = the number of nodes which produced primary laterals, the gross coefficients of correlation are

$$r_{ld} = .479 \pm .058$$

$$r_{nd} = .403 \pm .060$$

$$r_{nl} = .836 \pm .020$$

There is a significant degree of correlation between the number of nodes which produced primary laterals and the length of the branch. This means that longer branches have a tendency to produce more primary laterals than short branches, and speaks against the idea that a branch which attains more than average length is thereby incapacitated for producing a proportionally large number of laterals. There is nothing like a one to one correlation between length (or number of

nodes) and number of primary laterals, though the correlation is positive and significant. The correlation between length of branch and number of laterals may result largely from the close correlation between length of branch and total number of internodes on the branch. By calculating the coefficient of partial correlation we may eliminate the effect of the latter relation. The value is

$$r_{ln} = .283 \pm .070.$$

We may interpret this coefficient to mean that the greater length of branch favors lateral production, entirely apart from a greater number of nodes. The coefficient of partial correlation has a magnitude four times that of its probable error and may be regarded as significant. We may interpret it to mean that there is a small, but positive, degree of relationship between these two variables.

We may ask, Does the *proportionate* number of nodes producing laterals tend to change significantly with change in total number of nodes? The obvious suggestion, that we find the correlation between total number of nodes and percentage of nodes producing laterals, seems to involve the introduction of "spurious correlation of indices."

We may therefore compute the correlation between the number of primary laterals and the deviation of this number from its probable value

$$r_{nz} = \frac{r_{nd} - \frac{V_n}{V_d}}{\sqrt{1 - r_{nd}^2 + \left(r_{nd} - \frac{V_n}{V_d}\right)^2}}$$

In this case V_n and V_d are the coefficients of variability of the number of nodes and of the numbers of primary laterals respectively.

$$r_{nz} = -.082 \pm .075$$

The value of this coefficient is close to zero and, in view of the magnitude of its probable error, cannot be regarded as indicative of any correlation. It shows that there is little or no real difference in the proportionate capacity of branches with different numbers of nodes to produce primary laterals. In other words, there is no correlation between the number of primary laterals and the deviation from their probable number.

The lack of any marked causal relationship between the percentage of dormancy and the length of primary laterals is also indicated by the coefficient of correlation between these two characters. It has the very

low value of $r = .061 \pm .076$ and cannot be regarded as significant.

In figure 18, there is a presentation of the general problem of correlation in the apricot branch. The length and the number of primary laterals show a fairly high positive correlation with the length of the branches, and about the same degree of correlation with similar characters of the secondary laterals. The total length of all laterals bears a very high degree of positive correlation with the length of the branch.

VI. DIFFERENTIATION

1. CONFIGURATION OF LATERALS ON BRANCHES

The process of differentiation as manifested by the growth of primary and secondary laterals is one of the important aspects of this study. We are concerned, not alone with the activities which result in the formation of the main axis of the branch, but with the formation of its subsidiary shoots. These subsidiary shoots are morphological characters which go to make up the entities with which we are dealing. From the standpoint of the fruit grower they are of primary interest because they determine, to a large extent, the capacity of a branch to produce fruit. The importance of this process in Sea Island cotton has recently been discussed by Mason.⁴

The various groups of primary laterals on the apricot branches were so well delimited that it was an easy matter to determine and measure their salient characters. The data are summarized in table 9. Group I refers to the group nearest the proximal end of the branch, and group III to the group nearest the distal end (fig. 1). The length of the groups diminishes as we pass toward the distal end of the branches, and the space between groups increases.

The superior development of the laterals in Group I is most strikingly shown by a comparison of the total length of all primary laterals in that group with the length of primary laterals in other groups. In this respect Group I produced six times as much as Group II and seventeen times as much as Group III, while Group II produced only three times as much as Group III. The total number of nodes on primary laterals follows rather closely the ratios of total length.

The number of secondary laterals per branch borne upon the primary laterals of each group differs still more widely, as might be expected, since primary laterals must attain a certain size and stage of maturity before they produce secondary laterals.

TABLE 9
DATA ON THE LATERALS OF THE VARIOUS GROUPS

	MEANS		
	Group I	Group II	Group III
Length of group (cm.).....	75.00 ± 2.45	19.96 ± .81	10.94 ± .62
Number of node from which lowest primary lateral grew.....	16.32 ± .46	64.22 ± 1.41	101.35 ± 1.60
Total number of nodes in group.....	26.00 ± .87	7.32 ± .32	3.58 ± .21
Number of node from which highest primary lateral grew.....	47.08 ± .92	74.22 ± 1.50	106.35 ± .18
Time at which primary laterals appeared (weeks).....	4.31 ± .09
Total length of primary laterals in group.....	111.01 ± 54.55	188.18 ± 11.61	65.27 ± 4.34
Total number of nodes on primary laterals.....	675.32 ± 33.22	129.09 ± 7.66	45.77 ± 2.13
Mean number of primary laterals.....	25.54 ± .89	7.20 ± .33	4.00 ± .33
Length of primary laterals (cm.).....	49.20 ± .80	26.91 ± .92	18.09 ± 1.10
Mean number of secondary laterals.....	33.61 ± 2.53	1.86 ± .26	.19 ± .08
Length of secondary laterals (cm.).....	17.00 ± .29	17.00 ± .74
Mean number of blossoms.....	176.01 ± 8.15	41.08 ± 2.67	9.68 ± .86
Mean number of primary laterals which produced secondary laterals.....	5.11 ± .31

The time at which the first primary laterals were found upon the branches was recorded only for those of Group I. At that time (4.31 weeks) the mean length of the branches was about 70 cm. and they were approaching their period of most rapid growth.

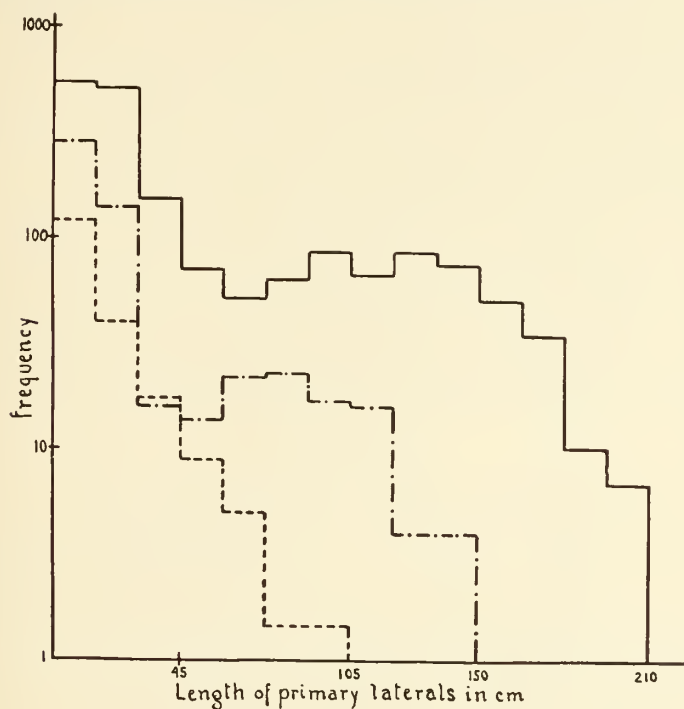


Fig. 8. Frequency distributions for length of primary laterals in the three groups plotted on logarithmic scales. Group I, —; Group II, -.-.-; Group III, -.-.

2. PRIMARY LATERALS

The frequency with which laterals of various lengths were produced is a matter of importance because it shows something of the ability of the main axis of the branches to produce new material. It is plain that the kind as well as the number of laterals produced is an index of the differentiation which occurred.

It has already been shown (figure 4) that the total length of all laterals, primary and secondary, *per branch* gives a skewed distribution. The figures in table 4 show that the coefficient of variability of the measurements of total length was rather high and indicate that the length distribution is subject to considerable fluctuation.

The histograms of length distribution for 2528 individual primary laterals (fig. 8) in the three groups are extremely asymmetric with

very high frequencies in the classes of shorter laterals. To appreciate fully the asymmetry of these distributions the reader must recollect that the frequencies are plotted on a logarithmic scale. The asymmetry appears to increase as one passes from Group I to Group III. Having seen the graphs representing the frequency distribution of laterals, the reader will appreciate the data in table 10 showing the mean length and variability of laterals of the various groups. The distributions show that the numbers of short laterals in the several groups are not governed by the laws of chance—they are indeed so far from what would occur in an approximately normal curve of errors that we must conclude that length of primary laterals is determined by some very definite factor so fixed in its action that the law of chance is practically eliminated. It is evident that more short laterals occurred in Groups II and III than in Group I, a result due in part, undoubtedly, to the age factor. Many of the laterals in these groups might have become longer if the growth cycle of the tree had not terminated when it did.

TABLE 10
LENGTH OF LATERALS ON APRICOT BRANCHES

	No. of vari- ants	Mean (cm.)	Standard deviation (cm.)	Coefficient of variability
Primary laterals, Group I..	1796	49.20 \pm .80	50.36 \pm .57	102.36 \pm 2.38
Primary laterals, Group II..	538	26.91 \pm .92	31.52 \pm .65	117.13 \pm 4.65
Primary laterals, Group III	194	18.09 \pm 1.10	22.75 \pm .78	125.76 \pm 8.79
Primary laterals, all groups.	2528	42.07 \pm .62	46.50 \pm .44	110.53 \pm 1.95
Secondary laterals, Group I	2276	17.00 \pm .29	20.22 \pm .20	118.94 \pm 2.33
Secondary laterals, Group II	156	17.00 \pm .74	13.72 \pm .52	80.70 \pm 4.68

As a further measure of the amount of differentiation we may determine the cases in which primary laterals produced secondary laterals. We have seen in table 4 that the mean number of secondary laterals per branch was 35 and table 9 shows that practically all of them arose on primary laterals of Group I. The number of primary laterals which produced secondary laterals was $5.11 \pm .31$ *per branch*, and the average number of secondary laterals on each was about six. As will be shown later, there is a high degree of positive correlation between the mean numbers per branch of primary and secondary laterals, which indicates that the same tendency toward differentiation is shared by branches and their laterals.

The total number of blossoms on the primary laterals shows differences somewhat similar to those of other characters. The number of blossoms on Group I was about four times as great as on Group II, and about eighteen times as great as on Group III.

TABLE 11

LENGTH OF PRIMARY LATERALS ON EACH DAUGHTER SHOOT

X = ordinal position of the laterals.

Y = average length of y_{x-1} , y_x , y_{x+1} .

X	Y (cm.)	X	Y (cm.)	X	Y (cm.)
2	0	53	10.95	104	1.05
5	.19	56	9.58	107	2.87
8	1.94	59	18.08	110	1.88
11	11.42	62	13.28	113	1.00
14	12.50	65	9.13	116	1.21
17	18.22	68	6.00	119	.98
20	26.36	71	2.92	122	.74
23	41.64	74	1.46	125	.38
26	52.40	77	1.08	128	.54
29	55.59	80	.58	131	.20
32	42.50	83	1.78	134	.0
35	29.60	86	.84	137	.08
38	21.80	89	1.51	140	.05
41	15.01	92	1.40	143	.04
44	8.72	95	1.22	146	.0
47	7.78	98	.63	149	.05
50	8.37	101	2.41	152	.05

We may attempt first to get a general idea of the number, position, and length of the primary laterals upon the branches under consideration. It has already been stated that the number of primary laterals ranged from 13 to 64 per branch with a mean of 37. The position of the primary laterals and the mean length of laterals in various positions may next be ascertained. These data are presented in table 11. The ordinal number of each primary lateral was determined by ascertaining the number of the node from which it grew, counting from the proximal (basal) end of the branch. The value of Y (the length of successive laterals) is recorded for the lateral in position X . In order to simplify the table, the mean length of three laterals is given for every third lateral; for example, the length Y was obtained by taking the average of y_{x-1} , y_x and y_{x+1} . The length of lateral 17 is accordingly the average length of laterals 16, 17, and 18.

The nodes at the base of the branches produced no laterals, or very short laterals. The length of the laterals was progressively longer as

the distance from the proximal end increased up to approximately lateral 30, then decreased rather rapidly to lateral 45. A second maximum occurred near lateral 60. From lateral 70 on to the distal end of the branch, the laterals were exceedingly variable in length, and the average for any given position is small. This may be, in part, because of the fact that they were produced later in the growing season and their growth was therefore terminated sooner by the approach of winter dormancy.

Casual observation will show that the primary laterals occur in well defined groups on each branch and that a true impression of the differentiation is not to be obtained readily from the figures presented in table 11. Most of the branches had three groups of primary laterals. The group nearest the proximal end of the branch was the largest, and, as already intimated, produced the longest primary laterals (cf. fig. 1). Above the first group, about 20 buds remained dormant, and the second group was inferior both in number and in length of laterals.

An analysis of the mean length of the primary laterals will be presented later in a discussion of certain dynamical aspects of their growth. We will now compare the primary laterals in the several groups with respect to their more obvious features.

The primary laterals in a group are rather symmetrically arranged according to length. The longest laterals are at the center of the groups and the lengths of other laterals diminish as one passes from the center to either end of the group. The rate at which the lengths of successive laterals diminish suggests a logarithmic curve.

All the groups were now superposed in such a way that the central lateral of each Group I fell upon the same point. If we take node 48 as the midpoint for the laterals of Group I, and arrange the data so that the actual centers of Group I coincide for all branches, we can easily get the mean length of the primary laterals for each node, upon the basis of a uniform arrangement. Table 12 gives the values so obtained. If this adjustment also results in placing the laterals of Groups II and III in symmetrically shaped groups, it might lend additional support to the assumption that the development of primary laterals is the outcome of a definite physiological function of growth. As a matter of fact, this is just what happens. The grouping of laterals in Group II results, on a smaller scale in the same arrangement as that in Group I. The arrangement of laterals in Group III is less striking on account of their shortness and because of their great variability, yet it is fairly definite.

TABLE 12

MEAN LENGTH OF PRIMARY LATERALS AFTER ADJUSTING POSITIONS SO THAT
BUD-POSITION 48 WAS THE CENTER OF GROUP I

X = ordinal bud-position.

Y = mean of y_{x-1} , y_x , and y_{x+1} .

X	Y	X	Y	X	Y
5	0.0	59	16.69	113	1.08
8	0.09	62	12.52	116	1.49
11	0.46	65	10.00	119	1.54
14	1.57	68	7.65	122	1.09
17	2.12	71	11.10	125	1.97
20	3.26	74	7.57	128	1.79
23	6.36	77	10.02	131	1.36
26	7.68	80	10.09	134	1.06
29	10.60	83	8.08	137	1.40
32	22.64	86	7.12	140	0.32
35	28.92	89	2.88	143	0.28
38	26.49	92	1.40	146	0.0
41	39.11	95	2.51	149	0.0
44	44.03	98	1.11	152	0.12
47	44.61	101	1.31	155	0.12
50	38.86	104	1.27	158	0.0
53	28.39	107	1.20	161	0.08
56	17.07	110	1.00		

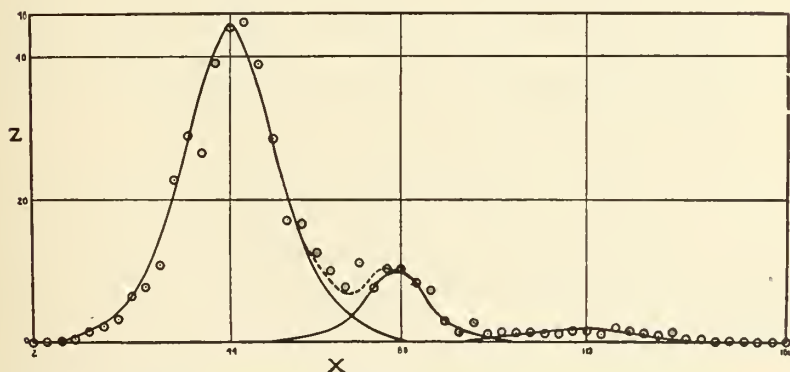


Fig. 9. Curves showing the cyclic nature of the three groups of primary laterals. X , ordinal position of laterals; Z , length of laterals. The curves were computed from the equations:

$$\begin{aligned} \text{Group I} & \dots\dots\dots Z_1 = .000177 y_1 (380 - y_1) \\ \text{Group II} & \dots\dots\dots Z_2 = .0017 y_2 (58 - y_2) \\ \text{Group III} & \dots\dots\dots Z_3 = .0024 y_3 (20 - y_3) \end{aligned}$$

The broken line represents the summation of overlapping portions of the curves of Groups I and II. Small circles represent mean lengths of laterals in the various ordinal positions after positions had been shifted to bring the center of each Group I to the same point.

Group I laterals had a maximum mean length of 44.6 cm. at node 48. The upper range of Group I overlaps the lower range of Group II, and it is necessary to recognize the overlapping values in studying the groups. This aspect will be discussed below. Node 70 probably marks the point near which Group I ends and Group II begins.

Group II laterals appear to reach a maximum mean length of about 10 cm. near node 80, from which point the length decreases to another minimum near node 98.

Group III appears to have a maximum mean length of laterals near node 119 from which the length decreases to near node 160.

The important feature, for our present purposes, is that the mean lengths of primary laterals fall into three distinct groups. When the values are plotted on a scale in which ordinates are the lengths of the several laterals and abscissae are the ordinal positions of laterals on the branch, they form three symmetrical, overlapping curves (fig. 9).

If we assume that the cyclic growth of the primary laterals is in some way similar to the cyclic growth in length of the branch which bears them, we may proceed to examine the data by the method already used. The situation may be simplified by assuming that the forces which produce the branches produce in the same way the primary laterals. The summations of length of laterals, beginning at the base of the branch, should therefore give a curve somewhat like that representing the increasing length of the branches, shown in figure 2. This was found actually to be the case, and the three groups of laterals could readily be distinguished. The observed values agreed closely with an equation of the general form

$$\log \frac{y}{a-y} = K (x - x_1)$$

where y = length at any node x ; x_1 = the node at which y had attained half the length of a for the cycle; a = the maximum (limiting) value of y ; and K = a constant.

If the lengths of the laterals be regarded as increments at unit distances on the branch, starting at the proximal end, then the differential form of the foregoing equation ought to express their lengths for each nodal position. The differential form of the above equation is

$$Z = \frac{dy}{dx} = ky (a - y)$$

$$\text{Here } k = \frac{K}{a}$$

With the aid of the table prepared by Robertson,¹³ the values of *Z* shown in table 13 were computed.

Group I $Z_1 = .000177 y_1 (380 - y_1)$
Group II $Z_2 = .0017 y_2 (58 - y_2)$
Group III $Z_3 = .0024 y_3 (20 - y_3)$

TABLE 13
MEAN LENGTH OF PRIMARY LATERALS SHOWING THEIR CYCLIC ARRANGEMENT.
VALUES OF *Z* WERE CALCULATED FROM THE EQUATIONS:

$Z_1 = .000177 y_1 (380 - y_1)$
 $Z_2 = .0017 y_2 (58 - y_2)$
 $Z_3 = .0024 y_3 (20 - y_3)$

GROUP I			GROUP II			GROUP III		
X	observed Y (cm.)	calc. Z ₁ (cm.)	X	observed Y (cm.)	calc. Z ₂ (cm.)	X	observed Y (cm.)	calc. Z ₃ (cm.)
8	.09	531	92	0
14	1.57	1.8	562	98	1.1	.3
20	3.26	4.2	594	101	1.3	.6
26	7.68	9.6	65	1.6	104	1.3	.9
32	22.6	20.7	71	11.1	4.8	110	1.0	1.2
38	26.5	35.7	74	7.6	8.1	116	1.5	1.5
44	44.0	44.1	78.8	9.9	119	1.5	1.8
50	38.9	35.7	80	10.1	9.6	122	1.1	1.5
56	17.1	20.7	86	7.1	5.4	128	1.8	1.2
62	12.5	9.6	92	1.4	1.8	134	1.1	.9
68	7.7	4.2	98	1.1	.6	140	.3	.6
71	2.7				146	.0	.3
						152	.1	.0

The values obtained from these equations indicate the cyclic nature of the growth process which governs the production of primary laterals. The curve (fig. 9) which represents the mean length of laterals in any group is symmetrical about the maximum value. The margins of the second group overlap those of the adjoining groups, and the calculated values of the overlapping portions must be added to approximate the observed values.

The satisfactory agreement between observed and calculated values seems to justify the conclusion that the length of each primary lateral was a function of its position in its group, and, consequently, of its position on the branch. The size of the group may depend to an even greater extent upon its position on the branch. The growth processes concerned with the production of laterals therefore bring about a definite spatial distribution of mass.

The decreasing amplitude of the three curves suggests that the successive groups of laterals may represent damped oscillations of the growth process. The limits of the third group are too poorly defined, however, to afford satisfactory material for the study of this possibility.

3. SECONDARY LATERALS

The secondary laterals are another distinct feature of the differentiation process in growth. Arising on the primary laterals, their existence is naturally conditioned to some extent by the factors which govern the production of primary laterals and determine their length.

Figure 5 gives a graphical comparison of the frequency distributions of primary and secondary laterals. The frequency polygon representing the distribution of the secondary laterals has much the same range as that representing the primary laterals, but is completely asymmetrical. The figures given in table 4 show that the standard deviation of the population as computed very nearly equals the mean. In such a case the mean fails to represent the population. It seems logical to conclude from these facts that the number of secondary laterals per branch is strongly affected by some factor which tends to keep the number at a minimum, for while the number per branch ranged from 0 to 136, more than two-fifths of the branches had less than 15 secondary laterals each.

A classification of 2831 primary laterals with respect to the number of secondary laterals which each produced shows a still more asymmetrical distribution. The 483 secondary laterals on these branches were produced on 17.06 per cent of the primary laterals, leaving 82.94 per cent which produced none. The majority of primary laterals which produced secondary laterals produced less than five each.

The production of secondary laterals with respect to the groups of primary laterals, elsewhere described, may also be noted. The average number of secondary laterals per branch on the primary laterals of Group I was 33.61 ± 2.53 ; on those of Group II, $1.86 \pm .26$; and on those of Group III, $.19 \pm .08$. It is more than probable that the age factor was dominant in causing this distribution.

Viewed from either standpoint there is no evidence that the numbers of secondary laterals on these branches were governed by the laws of chance. On the contrary, there is evidence of some definite, active factor which tends to keep the buds on the primary laterals in a condition of dormancy until the end of the first year. The number of

primary laterals on a branch does not depart widely from the values to be expected from the normal-curve type of variability, although it is modified by the location and position of the branch (see tables 5 and 6). The distribution of secondary laterals appears, however, to be widely different from that of the primary laterals.

The influence of the position of the branch upon the mean number of secondary laterals produced was found to be important, although subject to considerable variability. The figures given (table 14) show little difference in the numbers produced on branches which made an angle of less than 60 degrees from the perpendicular, but there was a much smaller number produced on branches which approached a horizontal position. The variability in the number of secondary laterals produced by all classes of branches is very great and gives support to a suggestion, for which I am indebted to Dr. H. B. Frost, viz., that the physiological processes were very sensitive and were readily turned in either direction by factors of an external or of an internal nature.

TABLE 14
INFLUENCE OF POSITION OF BRANCH UPON NUMBER OF SECONDARY
LATERALS PRODUCED

Position of Branch	Mean	Standard deviation	Coefficient of variability
0°-30° from perpendicular	54.67 ± 8.72	38.82 ± 6.17	71.01 ± 16.02
30°-60° from perpendicular	48.11 ± 4.82	37.10 ± 3.40	77.11 ± 10.55
60°-90° from perpendicular	21.19 ± 2.26	21.70 ± 1.60	102.41 ± 13.10

In addition to the data showing the influence of the position of the branch, there are certain correlations which show something of the influence of internal factors upon the formation of secondary laterals. The coefficient of correlation between the mean numbers of primary and secondary laterals per branch is

$$r = .549 \pm .053.$$

This relationship might be expected on a priori grounds, since secondary laterals are produced only on primary laterals. It is logical to expect that an increase in the mean number of primary laterals per branch would, *ceteris paribus*, be followed by an increase in the number of secondary laterals (fig. 10).

The production of secondary laterals is obviously dependent upon the ability of the branch to overcome the conditions which determine dormancy. This concept relates merely to the number of buds which grew into secondary laterals, not to the size of laterals produced. So far as problems of differentiation are concerned release from dormancy is a matter of prime importance. Unless the potentiality of the bud can find kinetic expression, it counts for nothing in the further differentiation of the branch.



Fig. 10. Regression line of mean number of secondary laterals per branch on mean number of primary laterals.

The lengths of secondary laterals in Groups I and II have been studied with reference to their frequency and variability. So few secondary laterals were produced in Group III, that they were not included in the study. The frequency distributions are shown in figure 11 and exemplify a case of pronounced asymmetry. It will be remembered that the length distributions of primary laterals show a similar type of distribution. In both cases it is apparent that, among the factors which determine the length of a lateral, the chance variations of the environment play a small part.

It is very interesting to note (table 9) that the mean length of secondary laterals in Groups I and II is the same in spite of the difference in age and position. The absence of any such relation in the primary laterals makes it doubtful whether there is any significance in this relationship, although it suggests that the forces involved in the growth of secondary laterals tend to come to a rather definite equilibrium.

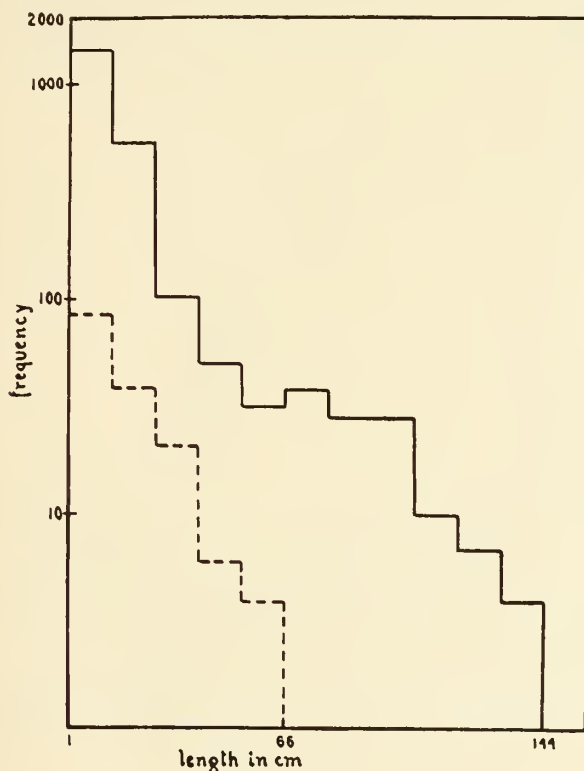


Fig 11. Frequency distributions for length of secondary laterals in Groups I and II, plotted on logarithmic scales. Group I, —, Group II, - - -.

The relation of the mean number of secondary laterals on a branch to their mean length expressed as a coefficient of correlation is

$$r = .148 \pm .078.$$

This coefficient is not large and, moreover, is only twice its probable error; consequently it fails to denote any significant correlation between the two variables. If the amount of unformed materials in the branch were more or less constant, we should then expect to find a definite negative correlation between these two variables, because

where few laterals were produced they would have more material to draw upon and consequently attain a greater size. The lack of any strong correlation shows that the size of the laterals is independent of any such factor. Indeed, if any weight be laid upon the coefficient, it must be interpreted in quite the opposite direction, i.e., the more laterals produced, the greater will be their average length. Doubtless this tendency would be more pronounced were it not for the fact that the manufacture of sufficient photosynthates is limited by the crowding and consequent shading of laterals during the growing season.

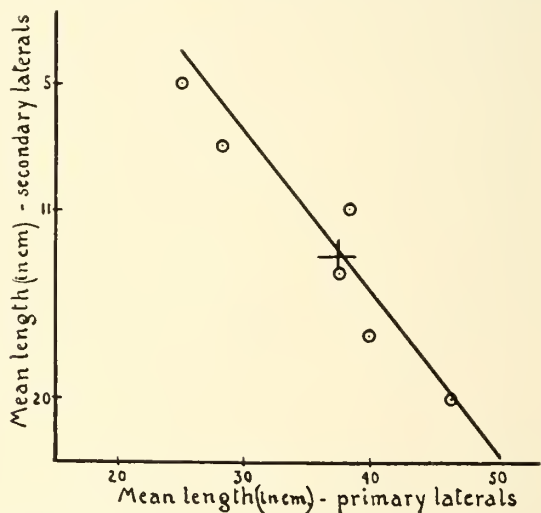


Fig. 12. Regression line of mean length (per branch) of secondary laterals on mean length of primary laterals.

Another important correlation is that which exists between the mean length of primary and secondary laterals of each branch. The coefficient expressing this correlation is

$$r = .467 \pm .062.$$

This expresses a strong positive correlation between the two variables and may be taken as evidence that the factors which determine the size of primary laterals on a branch operate in the same way on the secondary laterals. The validity of the correlation is shown by the linearity of regression (fig. 12).

This coefficient of correlation expresses concisely a relationship which was suggested by the rough parallelism of the polygons (fig. 5) showing the frequency distributions of the numbers of primary and secondary laterals per branch. Both distributions have the greatest frequencies in the region of the smaller numbers of laterals per branch.

4. BLOSSOMS

The formation of blossoms is an important stage in growth and differentiation. The blossom bud is a highly energized center on the vegetative organs toward which flow some of the most important synthetic materials from other parts of the tree. So far as the perpetuation of the species is concerned, the formation of a sufficient number of viable fruit buds is one of the factors of success in the struggle for existence. The horticulturist has an obvious interest in the factors which govern the formation of a maximum number of buds on fruit trees.

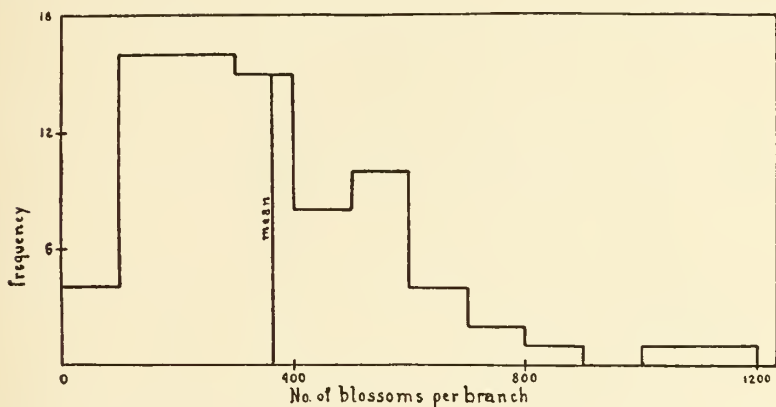


Fig. 13. Frequency distribution for number of blossoms on apricot branches.

The problem of fruit-bud formation on the apricot tree is broader than the aspects dealt with here, because most of the fruit buds are produced on laterals which appear after the branch is one year old. It is well known that such conditions are not favorable for the production of a maximum number of blossom buds. The problem here attacked is the production of fruit buds on branches which are making rapid vegetative growth in the first season.

The salient features of the number and variability of blossoms are shown in table 15 and in figure 13. The number of blossoms per branch ranged from 50 to 1200 with the mean at 360.26 ± 16.62 . The great variability in the number of blossoms per branch is shown by the frequency polygon and by the coefficient of variability of 60.39 ± 4.28 . This frequency polygon bears a certain resemblance to those representing the distribution of laterals, since it also has the highest frequencies in the region of a minimum number of blossoms per branch.

TABLE 15
THE PRODUCTION AND DISTRIBUTION OF FRUIT BUDS ON EACH BRANCH

	Mean	Standard deviation	Coefficient of variability
Total number of blossoms per branch.....	360.26 ± 16.62	217.55 ± 11.67	60.39 ± 4.28
Blossoms on main axis of branch.....	4.15 ± 0.49	6.50 ± .35	156.63 ± 20.44
GROUP I			
Blossoms on primary laterals.....	176.01 ± 8.15	107.41 ± 5.76	61.03 ± 4.33
Blossoms on secondary laterals.....	128.20 ± 9.89	130.33 ± 6.99	101.66 ± 9.55
GROUP II			
Blossoms on primary laterals.....	41.08 ± 2.67	35.22 ± 1.89	85.73 ± 7.23
Blossoms on secondary laterals.....	8.86 ± 1.43	18.81 ± 1.01	212.30 ± 36.05
GROUP III			
Blossoms on primary laterals.....	9.68 ± 0.86	11.34 ± .61	117.15 ± 12.20

The main axis of the branch bore very few blossoms, the majority of them being produced upon primary laterals.

The primary laterals of Group I produced the greater part of the blossoms and the variability of the mean number per lateral is less than in the more distally located groups. The variability of the means in all these groups is relatively enormous.

The decrease in the number and the increase in the variability of the numbers of blossoms in the distal regions of the branches may be due to a number of causes, among which we must recognize growth. While the distal region was growing, the physiological functions of that part were opposed to the formation of the energy centers which form blossom rudiments. In the proximal region, growth in mass had largely ceased so long before the end of the season that the development of blossom rudiments was not opposed by other functions. The effect of the migration and localization of materials in the branch is a biochemical question which will not be discussed here. Hooker^{2, 3} has made a significant beginning in the study of these factors and Barker and Lees¹ have approached the problem by a somewhat different route.

Since blossoms were produced mainly upon laterals, any factor which increases the production of laterals may also increase the production of blossoms. The coefficient of correlation between the number of blossoms per branch and the ratio of primary laterals to total number of nodes per branch is

$$r = .386 \pm .065.$$

This coefficient might be expected to measure the effect of the factors which overcome dormancy on the production of blossoms. One may assume that substances moving into the branch go either to the production of laterals or to the formation of flower rudiments. If, from any cause, the number of primary laterals were relatively small, the material might be used in forming flower rudiments. If the number of laterals were relatively large, they might so compete with flower-bud formation as to lessen the number of flowers formed; but this correlation coefficient speaks against the validity of such an assumption. The coefficient is positive and indicates that factors which cause the formation of numerous laterals also tend to form a larger number of flower buds. It is not improbable that the formation of primary laterals, through their ability to increase the amount of photosynthates, increases the formation of flower buds. Again, it is possible that the formation of the two kinds of units (laterals and flower buds) is an expression of the same tendency to differentiation.

The next step in this study was designed to answer the question, Is there any relation between the length of a lateral and the number of blossoms it bears? There is an opinion current that short laterals are the most precocious in fruiting habits. This opinion, however, may be due to the fact that the blossoms on them must of necessity be close together and are therefore more conspicuous. A more accurate idea of the relationship may be obtained by ascertaining the correlation coefficient between the number of blossoms and the number of nodes of the laterals.

Correlation coefficients were determined for 972 primary laterals in Group I, since this is the largest and most representative group of laterals. If

a' = number of blossoms on primary laterals

b' = number of nodes on primary laterals

c' = length of primary laterals

the coefficients of correlation are

$$r_{a'b'} = .089 \pm .020$$

$$r_{a'c'} = .077 \pm .020$$

$$r_{b'c'} = .969 \pm .014$$

The coefficient representing the correlation between the numbers of blossoms and nodes is small, and of very doubtful significance; the same holds true of the correlation between number of blossoms and length of lateral. The third coefficient shows, as one might predict, a very high correlation between the length of a lateral and the number of nodes it bears.

On the face of these coefficients of gross correlation, we should conclude that there is practically no association between the number of nodes and the number of blossoms a lateral may bear. The problem is a bit complicated by the fact that the laterals are of different lengths, but this factor may be eliminated by making the partial correlation between the numbers of buds and nodes.

$${}_{a'b'}r_c = .059 \pm .021$$

This coefficient shows very plainly that there is no correlation between the number of blossoms and the number of nodes on the laterals. That is to say, a short lateral may have as many blossoms as a long lateral.

The character of the correlation coefficient may be made a bit plainer by referring to the curve of means of y_x in figure 14, which shows the mean number of blossoms produced upon the laterals

possessing varying numbers of nodes. The curve of the means of blossoms for primary laterals shows that we are not here dealing with a case of linear regression and that the coefficient of gross correlation is therefore somewhat lacking in reliability. It is interesting to note that the greatest mean number of blossoms occurred on laterals bearing from 30 to 60 nodes.

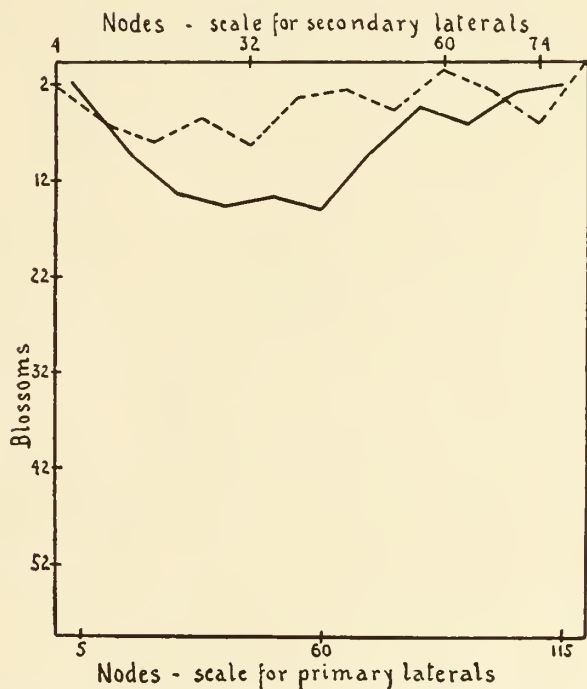


Fig. 14. Relation of the number of blossoms to the number of nodes. Curves of the means of y_x . Primary laterals, —; secondary laterals, - - -.

A better idea of the relations between the two characters may be grasped from the representation of the blossom-node distribution as shown in figure 15. This blossom-node surface shows that there are two kinds of primary laterals on apricot branches. The larger class has a tendency toward a linear regression of blossoms on nodes, i.e., the more nodes the more blossoms. It is true that the ellipses showing the distribution values are imperfect, but that is because the frequency distributions of these values are so asymmetrical (fig. 13). The smaller class of laterals is indicated by the partial ellipses in the upper right portion of the blossom-node surface. These laterals were characterized by many nodes and few blossoms. This blossom-node surface there-

fore shows clearly that the apricot branches possessed a large number of fruiting laterals and a smaller number of vegetative laterals. It also shows why the curve of means of y_x has an upward trend in the nodal classes of high values.

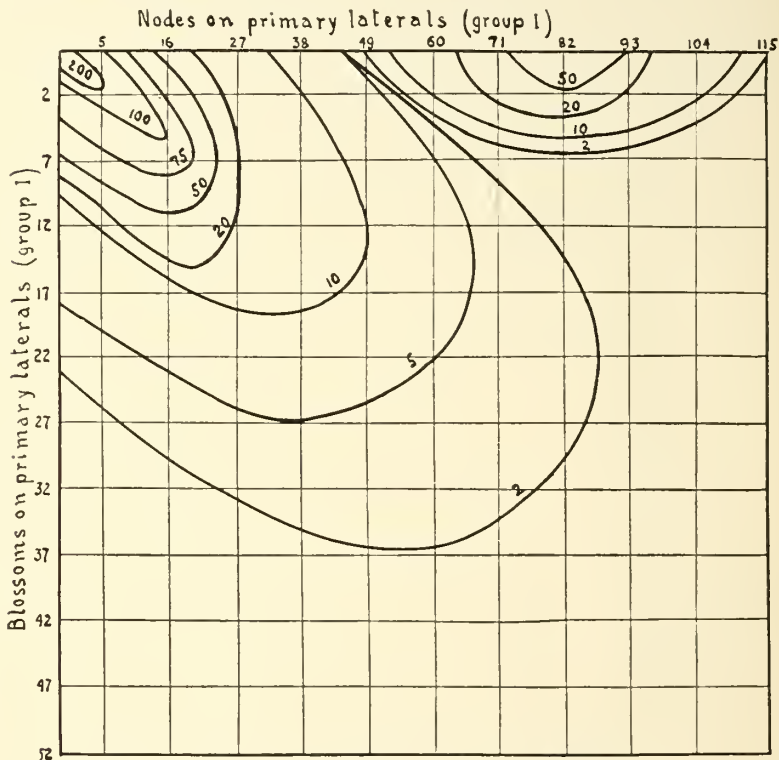


Fig. 15. Blossom-node surface for primary laterals.

The blossoms on the secondary laterals borne on primary laterals of Group I were also studied in somewhat the same manner. The frequency distributions of blossoms and nodes on the secondary laterals were of the same asymmetrical types as on the primary laterals and the coefficients of gross correlation were similar.

The following notation was used:

- a'' = number of blossoms on secondary laterals
- b'' = number of nodes on secondary lateral
- c'' = length of secondary lateral

The coefficients of correlation as determined for a population of 1370 secondary laterals were

$$\begin{aligned} r_{a''b''} &= .118 \pm .018 \\ r_{a''c''} &= .122 \pm .018 \\ r_{b''c''} &= .971 \pm .001 \end{aligned}$$

The first two coefficients are somewhat more reliable than the corresponding determinations on primary laterals, but they cannot be regarded as indicating any strong degree of association between the characters concerned. Indeed, it is evident from other relations that the number of blossoms a secondary lateral bore was quite independent of the number of nodes or of its length. The coefficient of partial correlation is

$$a''_b r_{c''} = -.002 \pm .018$$

In view of the fact that the value of this coefficient is practically zero, it is evident that if all the secondary laterals were of equal length, there would be no correlation between the numbers of blossoms and nodes upon them.

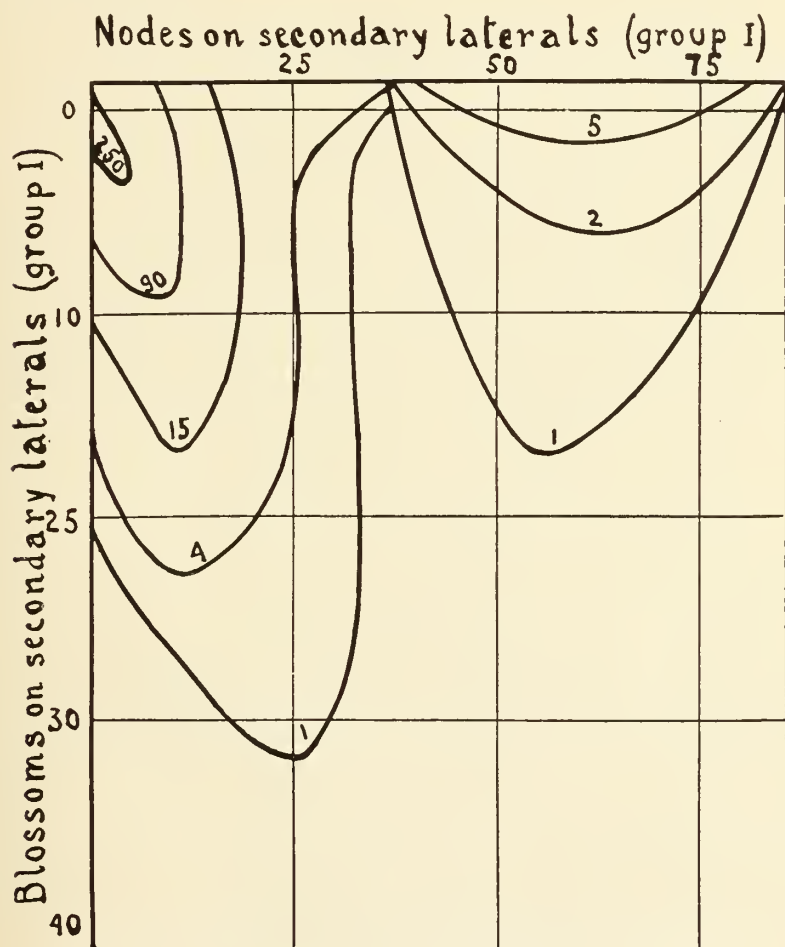


Fig. 16. Blossom-node surface for secondary laterals.

The curve of the means of y_x (fig. 14) shows that the mean numbers of blossoms on classes of laterals with varying numbers of nodes were not significantly different, in fact, they were remarkably constant. The actual range for values of y_x was 0 to 8.16. It is evident from these values that we are not dealing with a case of linear regression between these two characters.

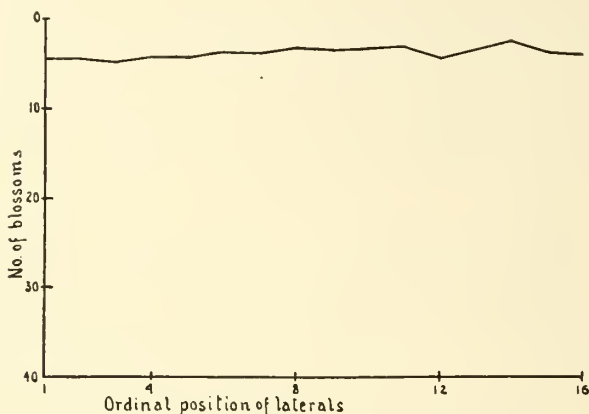


Fig. 17. Relation of the number of blossoms to the position of the secondary lateral on which they were borne. Curve of the means of y_x .

The actual distribution of blossoms on the secondary laterals is well shown by figure 16. Here, again, we see that there are two rather distinct classes of laterals, one of which bore many more blossoms in proportion to the number of nodes than the other. The first class includes laterals having less than 40 nodes and the partial ellipses representing their distribution have axes sloping rather steeply downward. The other group which contains long laterals appears to be distinctly vegetative in character; at least, it bore relatively few blossoms in proportion to its number of nodes.

One further aspect of the distribution of blossoms was investigated, viz., the correlation between the position of a secondary lateral and the number of blossoms it bore. It is interesting to know whether the lower laterals in a group produced more or less blossoms than the upper laterals. The records of 2011 secondary laterals on primary laterals of Group I were used in making the correlation table. They were counted in succession, the lateral nearest the base of the primary lateral on which they were borne being designated as number one. The coefficient of correlation between these variables was

$$r = -.109 \pm .022.$$

It indicates only a small degree of negative correlation and may be interpreted to mean that the lower laterals were only slightly if at all superior to others in the production of blossoms.

The remarkable uniformity in the mean number of blossoms on laterals is shown by the means of y_x (fig. 17). From this we may infer that it was neither the number of nodes on a lateral nor the ordinal position of the lateral which determined the number of blossoms it bore, but some other, as yet, unknown factor.

VII. GENERAL SURVEY OF CORRELATED VARIABILITY IN THE APRICOT BRANCH

The method of presenting correlations employed in figure 18 gives a comprehensive idea of the relations existing between the variables whose correlation has been discussed on widely separated pages. The manner in which the coefficients are shown on the lines which connect the names of the characters whose correlation was determined calls for little additional discussion.

The length of the branch was employed as the central character from which others radiate, since the length of that member seems to be an excellent index of growth. The majority of the coefficients are large enough in comparison with their probable errors to be significant. In the cases where one variable is very dependent upon another, e.g., where the number of nodes depends almost entirely upon the length of the laterals, the coefficient of correlation between the two variables is very high.

VIII. SUMMARY

1. The pattern of the organism is the result of a process of growth and differentiation which is largely an expression of inherent factors. Growth and differentiation lead to a quantitative distribution of matter in space that makes it necessary to regard the position and size of members of the branches as the expression of an inherent tendency which varies within limits under the influence of the ever-varying environment.

2. The main axis of the apricot branch shows distinct cycles of growth during the first season, each of which may be expressed by a logarithmic equation similar to that of autocatalysis. The maximum rate of growth was reached in the fifth and sixth weeks.

3. The branches in the population studied were less variable in length than in any other character. Their frequency polygon for length is fairly symmetrical with respect to its mean and does not depart widely from the type of polygon which represents a chance distribution of characters in biological material. The mean length of all laterals was more than seven times that of the branches on which they were borne. The degree of association between number of laterals per branch and the length of the branch was not high; but it was high between the length of branch and length of laterals it bore. The location of the branches and their angle with the perpendicular had certain effects upon their growth and differentiation. Branches on the north side of the tree produced the maximum number of primary laterals and blossoms. Branches which made an angle of 60 to 90 degrees with the perpendicular had fewer laterals and blossoms than those which were more nearly upright, although the ratio of blossoms to unit length of lateral was greater on the horizontal branches.

4. The distribution of laterals and blossoms showed wide divergence from the normal frequency distribution of variables. Groups containing the smaller numbers of laterals and blossoms per branch had by far the greatest frequencies. The types of distribution here studied appear to depend, not upon the chance factors of the environment, but upon fundamental internal conditions of differentiation. These internal conditions are obviously grounded in the basic growth tendencies of the cells, that is to say, in their genetic constitution, and are especially conditioned by certain inescapable spatial limitations. A striking result of these conditions is that relatively large growth occurs in a few buds and shoots, while relatively slight growth (or none) occurs in many buds and shoots. We find, therefore, a general tendency toward distributions showing positive skewness, with or without zero classes. The close approach in this study to a Gaussian distribution for 'branch' length is doubtless due to the method of initial sampling; only shoots in favorable locations were selected for study, and the feebler majority was thus eliminated.

5. Most of the nodes remained dormant through the first season. The ratio of nodes which produced laterals is such that it indicates a cyclic distribution of the forces which break the dormancy of lateral buds.

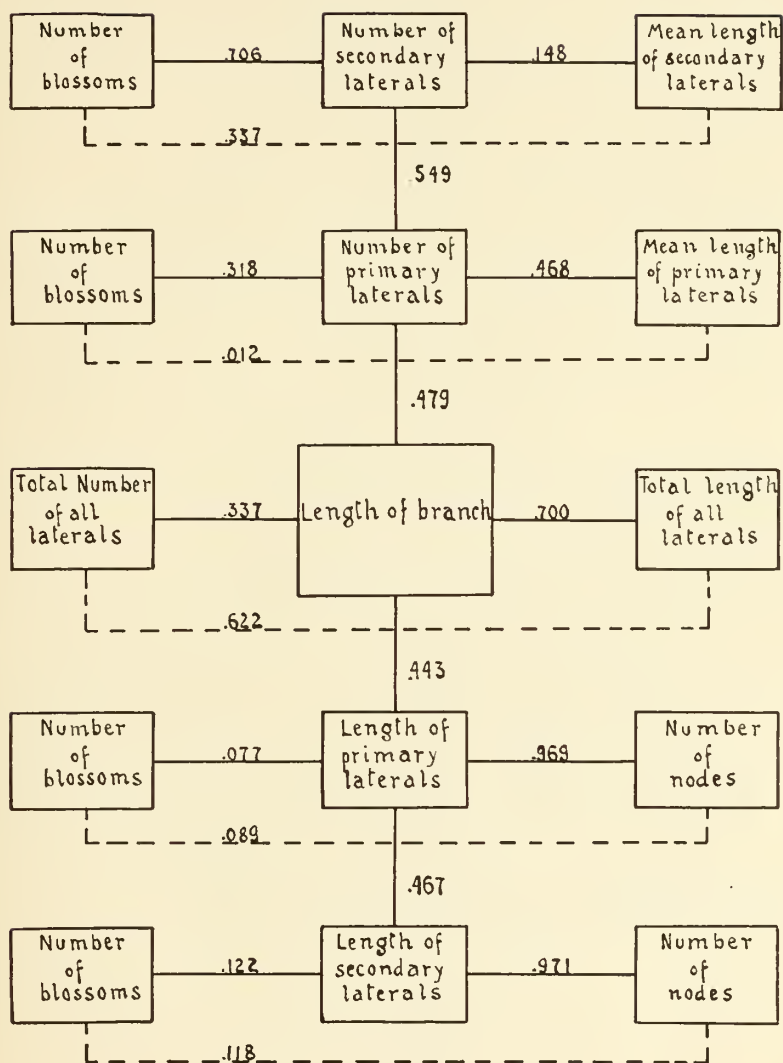


Fig. 18. Diagram representing correlations between certain characters.

6. The configuration of primary laterals on the branch afforded suitable material for the study of the statics of cyclic growth and gave satisfactory evidence of a definite distribution of matter in space. The production of material for the formation of laterals appears to follow the same mathematical relations as does the growth of the branch. A method is described by which it was possible to compute the length of a lateral situated at a given node.

7. The general form of frequency distribution of the numbers and lengths of secondary laterals does not appear to be conditioned to any great extent by the factors located in the environment. The mean number of secondary laterals per branch showed rather a high positive correlation with the mean number of primary laterals. The correlation between the mean number of secondary laterals and their mean length indicated that the size of the laterals is not dependent upon the factors which determine their numbers. The mean lengths of primary and secondary laterals on a branch showed a correlation which indicated that the factors which operated to determine the length of one order of laterals acted similarly on the other class.

8. The main axis of the branch produced very few blossoms in the following season; the primary laterals bore the majority of those produced. The mean number of blossoms per lateral tended to be rather constant regardless of the length of the lateral, and indicates that random factors of the environment were less important than internal factors of differentiation in determining distribution. The blossom-node surface gave good evidence of the occurrence of two classes of laterals on apricot branches; the larger class showed a tendency toward a linear regression of blossoms on nodes, while the smaller class was characterized by the possession of many nodes and few blossoms, and showed no definite tendency toward linear regression.

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